

# Population Metabolism of Millipedes at Two Altitudinal Zones in the Central Alps (Tirol, Austria)

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## ABSTRACT

The respiratory metabolism of *Enantiulus nanus* (LATZEL, 1884) from a mixed oak wood (670 m a.s.l.) and of 3 subalpine species, *Leptoiulus saltuvagus* (Verhoeff, 1898), *Ochogona caroli* (Rothenbühler, 1900) and *Haasea fonticulorum* (Verhoeff, 1910) from an *Alnus viridis* community (2000 m) was measured using a Gilson respirometer and a Warburg respirometer with electronic manometers. Temperature (6-20°C) and mass-specific (*E. n.*: 2-17 mgfw; *L. s.*: 3-75 mgfw; *O. c.*: 1-10 mgfw; *H. f.*: 2-12 mgfw) oxygen consumption values of these species are presented. The lowland species has its greatest sensitivity to temperature changes between 10°C and 15°C, the subalpine species between 6°C and 10°C with  $Q_{10}$ -values between 3.1 and 7.9. Based on a mean *E. nanus*-biomass of 2.9 g fresh mass per m<sup>2</sup> (= 73% of the total millipede-biomass) in the oak wood, the population metabolism of this species equalled 1488 ml O<sub>2</sub> m<sup>-1</sup> and year (= 30 KJ). In contrast a total millipede biomass of 2.2 g fresh mass per m<sup>2</sup> in the subalpine site respire only 732 ml O<sub>2</sub> m<sup>-1</sup> and year (= 15 KJ). The most important single factor in determining the metabolism for field populations is its population structure and biomass.

## RÉSUMÉ

**Métabolisme de populations de diplopedes dans deux zones altitudinales des Alpes Centrales (Tyrol, Autriche).**

Le métabolisme respiratoire de *Enantiulus nanus* (Latzel, 1884) d'une forêt mixte de chêne (altitude 670 m) et de trois espèces subalpines, *Leptoiulus saltuvagus* (Verhoeff, 1898), *Ochogona caroli* (Rothenbühler, 1900) et *Haasea fonticulorum* (Verhoeff, 1910) d'un peuplement à *Alnus viridis* (altitude 2000 m) a été mesuré à l'aide d'un respiromètre de type Gilson et d'un respiromètre de type Warburg équipés de manomètres électroniques. On donne ici les températures (6-20°C), les masses spécifiques fraîches (*E. n.* : 2-17 mg mf; *L. s.* : 3-75 mg mf; *H. f.* : 2-12 mg mf) et les valeurs respectives de consommation en oxygène. L'espèce de plaine présente une plus grande sensibilité aux changements de température entre 10°C et 15°C, les espèces alpines entre 6°C et 10°C, avec des valeurs de  $Q_{10}$  variant de 3,1 à 7,9. En se basant sur une biomasse moyenne pour *E. nanus* égale à 2,9 grammes de matière fraîche par mètre carré (qui représente 73% de la biomasse totale des diplopedes) dans la chênaie, le métabolisme respiratoire annuel de cette population équivaut à 1488 ml O<sub>2</sub> m<sup>-1</sup> (= 30 KJ). En comparaison, une biomasse totale de diplopedes de 2,2 g de matière fraîche par mètre carré ne représente, dans les sites subalpins, qu'une respiration de 732 ml O<sub>2</sub> m<sup>-1</sup> (= 15 KJ). Le facteur le plus important dans le déterminisme du métabolisme respiratoire des populations sur le terrain semble être la structure du peuplement et la biomasse.

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## INTRODUCTION

In a recent contribution PENTEADO *et al.* (1991) have summarized available data on oxygen consumption in millipedes. Respiratory rates of more than 20 species living in temperate or tropical regions, ranging in size from 10 to 4000 mg have been evaluated and discussed in relation to size of individual and sex. Further variables such as temperature, life stages or decreased oxygen tension have been investigated in numerous papers such as DWARAKANATH (1971), GROMYSZ-KALKOWSKA (1970, 1973), GROMYSZ-KALKOWSKA & STOJALOWSKA (1966) or PENTEADO & HEBLING-BERALDO (1991). Data on oxygen consumption rates of millipedes in context with the life-cycle and population structure are rare. WOOTEN & CRAWFORD (1974) gave such an example by combining monthly measurements of the respiration rate of a desert millipede with its behaviour in the field.

The aim of the present paper is to combine detailed laboratory investigations of the respiratory rates of four alpine millipede species (FISCHER, 1985; MARSONER, 1992) with the results from studies on the population structure, life-cycle and temperatures in their habitats (MEYER, 1979, 1985; KOFLER & MEYER, 1992). In this way it is possible to evaluate the relative importance of variables such as age structure, biomass, time of the year, temperature and altitude affecting the population metabolism in the field.

## MATERIAL AND METHODS

Specimens of *Enantiulus nanus* (Latzel) (2-17 mg live mass) were collected from an inneralpine mixed oak wood (670 m a.s.l.) in the Inn-valley near Stams at four occasions between October 1990 and October 1991. The life-history, abundance and production of this species have been studied in detail by KOFLER & MEYER (1992). The annual mean abundance of *E. nanus* is 859 inds m<sup>-2</sup> and this species dominates the total millipede fauna in this oak wood. Males reach maturity first as stadium VIII in the 3rd year, females also become adult with stage VIII and lay eggs after the third overwintering. This iteroparous julid species shows a seven-year life-cycle. A mean overwintering biomass of 2.9 g fresh mass m<sup>-2</sup> produces 1.5 g fresh mass m<sup>-2</sup> year<sup>-1</sup>. The animals were kept in plastic boxes provided with tap water agar to maintain a near 100% humidity and fed dead leaves. These cultures were maintained at field-like conditions with fluctuating temperatures (night/day): March, April and October: 7.5°C/12.5°C, May, June and September: 12.5°C/17.5°C, July and August: 17.5°C/22.5°C, November: 2.5°C/7.5°C. Approximately 470 inds of *E. nanus* were used in the assessment of respiratory metabolism between March and November 1991. Experimental temperatures were: 5°C (November), 10°C (March, April, October), 15°C (May, June, September) and 20°C (July and August). Rates of oxygen uptake of individual specimens were measured using a Warburg respirometer with electronic manometers connected to a module box and a PC. During each experiment 13 respirometer flasks (Volume: 2.2-2.6 ml) contained animals and one acted as a thermo-barometer-control. In each flask CO<sub>2</sub> was absorbed by a 5% solution of NaOH (20 µl) pipetted into the lower part of a two-piece flask. The animals were placed into the upper part of the flask which had a sintered floor to allow gas exchange. A high humidity was maintained by inserting a damp and crumpled piece of filter paper. After introducing the individuals into the flasks an half hour settling period was allowed to elapse before closing the respirometer valves. Each experiment lasted at least 24 h. At the end of the experimental period the millipedes were weighed individually. Oxygen consumption was calculated from a series of usually 144 measurements (10 min measuring intervals) by excluding the first hour (6 measurements) after closing the valves.

Specimens of *Leptoilulus saltuvagus* (Verhoeff) (3-75 mg life mass), *Ochogona caroli* (Rothenbühler) (1-10 mg life mass) and *Haasea fonticolum* (Verhoeff) (2-12 mg life mass) were collected from an *Alnetum viridis* (2000 m a.s.l.) in the Ötztal Alps near Obergurgl at several occasions between August and October 1984. Previous investigations by MEYER (1979, 1985) established for *L. saltuvagus* a mean density of 209 inds m<sup>-2</sup> and a biomass 1.2 g fresh mass m<sup>-2</sup>. The semelparous julid species reaches maturity in stage IX, X or XI after four or five years. At the same site the two chordeumatid species have a mean density of 112 inds m<sup>-2</sup> (*O. caroli*) and 107 inds m<sup>-2</sup> (*H. fonticolum*). This corresponds with a mean biomass of 0.42 g fresh mass m<sup>-2</sup> (*O. c.*) and 0.63 g fresh mass m<sup>-2</sup> (*H. f.*). A three-year life-cycle is probable for both chordeumatid species.

The animals were kept in light-temperature chambers representing approximately field conditions (day/night-temperature: 12°C/8°C, 12/12 h) in plastic boxes provided with tap water agar to maintain a near 100% humidity and fed dead leaves. Approximately 80 individuals of *L. saltuvagus* and 40 individuals each of *O. caroli* and *H. fonticolum* were used in the assessment of respiratory metabolism. Between July 1984 and February 1985 rates of oxygen uptake of individual specimens of the three species were measured using a refrigerated GR-14 Gilson differential respirometer. Measurements were made at 6°C, 10°C, 15°C and 20°C. During each experiment 9-12 respirometer flasks (Volume: 25 ml) contained animals and three acted as controls. In each flask CO<sub>2</sub> was absorbed by 5N NaOH pipetted onto a roll of filter paper held in the centre well. A perforated plastic cylinder placed over the central wall prevented the animals making contact with the NaOH. A high humidity was maintained with moist filter paper on the floor of the chamber. Two damp

and crumpled 1 cm<sup>2</sup> pieces of the same material provided shelter and the animals usually became quiescent within 1 h of being placed in the vessels. Because of the respirometer response and precision, 3 individuals of the smallest size classes were placed in each chamber.

Temperatures in the litter layer of the two sites were recorded with a Goerz Thermoscript (clockwork mechanism and bimetallic probe).

## RESULTS

### *The relationship between respiratory rate and size of individual*

#### *Enantiulus nanus* (Latzel, 1884)

As indicated in Table 1, the smallest specimens of *E. nanus* consume at least twice as much oxygen per unit mass than the largest ones at all experimental temperatures between 5°C and 20°C. The b-values according to the equation  $R = a W^b$  where R is the respiratory rate expressed in  $\mu\text{l}$  oxygen ind<sup>-1</sup> are scattered between 0.012 (5°C, Nov.), 0.205 (10°C, Oct.), 0.236 (15°C, June), 0.306 (20°C, Aug.), 0.329 (15°C, May), 0.441 (15°C, Sept.) and 0.488 (20°C, July) depending on temperature and time of the year.

TABLE 1. — Mean ( $\bar{x} \pm \text{S.E.}$ ) rates of oxygen consumption per unit mass ( $\mu\text{l mg}^{-1} \text{ h}^{-1}$ ) over the size range of *Enantiulus nanus* at 5°C, 10°C, 15°C and 20°C.

Size range (mg)	n	5°C	n	10°C	n	15°C	n	20°C
1.6 - 4.9	6	0.09±0.01	6	0.13±0.03	11	0.21±0.03	4	0.22±0.03
5.0 - 6.9	4	0.05±0.01	12	0.08±0.01	30	0.14±0.01	17	0.14±0.01
7.0 - 10.9	11	0.04±0.01	25	0.06±0.01	43	0.11±0.01	19	0.12±0.01
11.0 - 16.6	4	0.03±0.01	13	0.05±0.01	33	0.08±0.01	16	0.10±0.01

#### *Leptoiulus saltuvagus* (Verhoeff, 1898)

Table 2 shows the respiratory rates of *L. saltuvagus*. Again juveniles consume considerably more oxygen per unit mass than adults. The calculated b-values are between 0.67 (10°C), 0.68 (20°C), 0.82 (15°C) and 0.92 (6°C).

TABLE 2. — Mean ( $\bar{x} \pm \text{S.E.}$ ) rates of oxygen consumption per unit mass ( $\mu\text{l mg}^{-1} \text{ h}^{-1}$ ) over the size range of *Leptoiulus saltuvagus* at 5°C, 10°C, 15°C and 20°C.

Size range (mg)	n	6°C	n	10°C	n	15°C	n	20°C
3.0 - 16.0	6	0.08±0.01	16	0.18±0.01	5	0.21±0.03	7	0.36±0.03
17.4 - 74.8	9	0.07±0.01	14	0.11±0.01	8	0.15±0.01	7	0.21±0.04

#### *Ochogona caroli* (Rothenbühler, 1900)

Mass specific oxygen consumption rates of *O. caroli* (Table 3) indicate higher values for juveniles than for adults. Depending on temperature b-values range between 0.60 (6°C), 0.66 (15°C), 0.81 (10°C) and 0.83 (20°C).

TABLE 3. — Mean ( $\bar{x} \pm \text{S.E.}$ ) rates of oxygen consumption per unit mass ( $\mu\text{l mg}^{-1} \text{ h}^{-1}$ ) over the size range of *Ochogona caroli* at 5°C, 10°C, 15°C and 20°C.

Size range (mg)	n	6°C	n	10°C	n	15°C	n	20°C
1.2 - 3.2	7	0.16±0.01	5	0.24±0.03	7	0.30±0.06	11	0.32±0.02
5.1 - 10.3	8	0.09±0.01	9	0.17±0.02	9	0.17±0.01	8	0.27±0.04

*Haasea fonticolum* (Verhoeff, 1910)

The rates of oxygen consumption per unit mass over the size range of *H. fonticolum* (Table 4) indicate unexpectedly high values for the adults. Even the calculated b-values ranging between 0.94 (6°C), 1.41 (15° and 20°C) and 1.67 (10°C) do not show the expected relationship between oxygen consumption and size of the individuals. However, the evident activity peak of adult *H. fonticolum* between September and November known from pitfall trapping (MEYER, 1979) may be responsible for the extraordinary respiration rates as the experiments were carried out between 20th Sept. and 12th Dec.

TABLE 4. — Mean ( $\bar{x} \pm S.E.$ ) rates of oxygen consumption per unit mass ( $\mu\text{l mg}^{-1} \text{h}^{-1}$ ) over the size range of *Haasea fonticolum* at 5°C, 10°C, 15°C and 20°C.

Size range (mg)	n	6°C	n	10°C	n	15°C	n	20°C
1.9 - 4.6	3	0.09±0.02	5	0.17±0.05	7	0.19±0.02	3	0.28±0.05
5.4 - 11.8	8	0.10±0.01	8	0.25±0.01	7	0.30±0.02	5	0.45±0.03

*The relationship between respiratory rate and temperature*

This relationship was investigated using specimens that had been reared at quasi field temperatures throughout the year and measured at corresponding experimental temperatures of 5°C, 10°C, 15°C and 20°C. The results given in Tables 1-4 and Figures 2-5 indicate that oxygen consumption rates of the four species investigated do not gradually increase with increasing temperature. In *E. nanus* the steepest increase in oxygen consumption takes place between 10°C and 15°C which can be summarised as a  $Q_{10}$  value of 3.08 (mean over all size classes). Between 15°C and 20°C the respiratory metabolism is nearly balanced ( $Q_{10} = 1.21$ ). In the three subalpine species (*L. saltuvagus*, *O. caroli* and *H. fonticolum*) the independence of their respiratory metabolism of the temperature lies between 10°C and 15°C. In all cases the  $Q_{10}$  values are not significantly different from 1 (MANN-WHITNEY test). Between 6°C and 10°C the relationship between respiratory rate and temperature is very close with  $Q_{10}$  values of 7.9 (*L. saltuvagus*), 3.2 (*O. caroli*) and 7.2 (*H. fonticolum*).

*Variation in respiratory rate with season*

Measurements of the respiratory metabolism of *E. nanus* were carried out during the period between April and November. The experimental temperatures corresponded to the rearing temperatures and those to the temperature in the litter layer of its habitat. Hence in April and October the experimental temperature was 10°C, in May, June and September 15°C, in July and August 20°C and in November 5°C. In Figure 1, the respiratory rates at corresponding experimental temperatures but different months are compared.

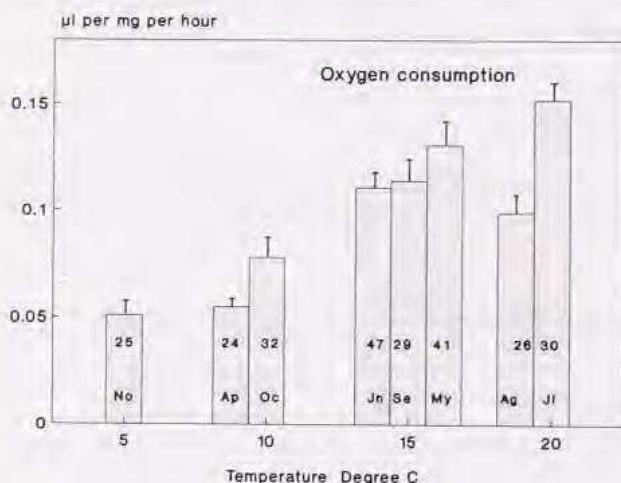


FIG. 1. — Mean ( $\bar{x} \pm S.E.$ ) respiratory rates of *Enantiulus nanus* at different temperatures and seasons. The letters within the columns indicate the month in which the respiration experiments at the given temperature were made. The figures within the columns indicate the number of animals used.

Relating results to the season (months), there is no significant difference in the respiratory rate of *E. nanus* at 10°C and 15°C. Only in August at the given temperature of 20°C did the animals respire at a significantly lower rate than in July. That corresponds with the life cycle of *E. nanus*. Adults undergo their annual moulting phase in August and are therefore inactive.

### Estimation of population metabolism

PHILLIPSON (1970) recommended a "best estimate" of respiratory metabolism as the mean energy loss per unit mass per unit time calculated from laboratory measurements on all life stages of a given species. Its calculation is independent of field population data, fluctuations in field temperatures and generation time. During this investigation, oxygen consumption of all life stages of four millipede species has been measured at temperatures of 5°C, 10°C, 15°C and 20°C. The results are summarised in Tables 1-4. Estimates of population metabolism have been obtained by multiplying the size- and temperature- specific respiratory rates with the time- and age- specific biomass data from the field (Figs 2-5). It should be mentioned that the temperature specific respiration rates were calculated on the basis of the  $Q_{10}$  values and not on the assumption that respiratory rate is an exponential function of temperature, as was demonstrated by HASSALL (1983) for the isopod *Philoscia muscorum*.

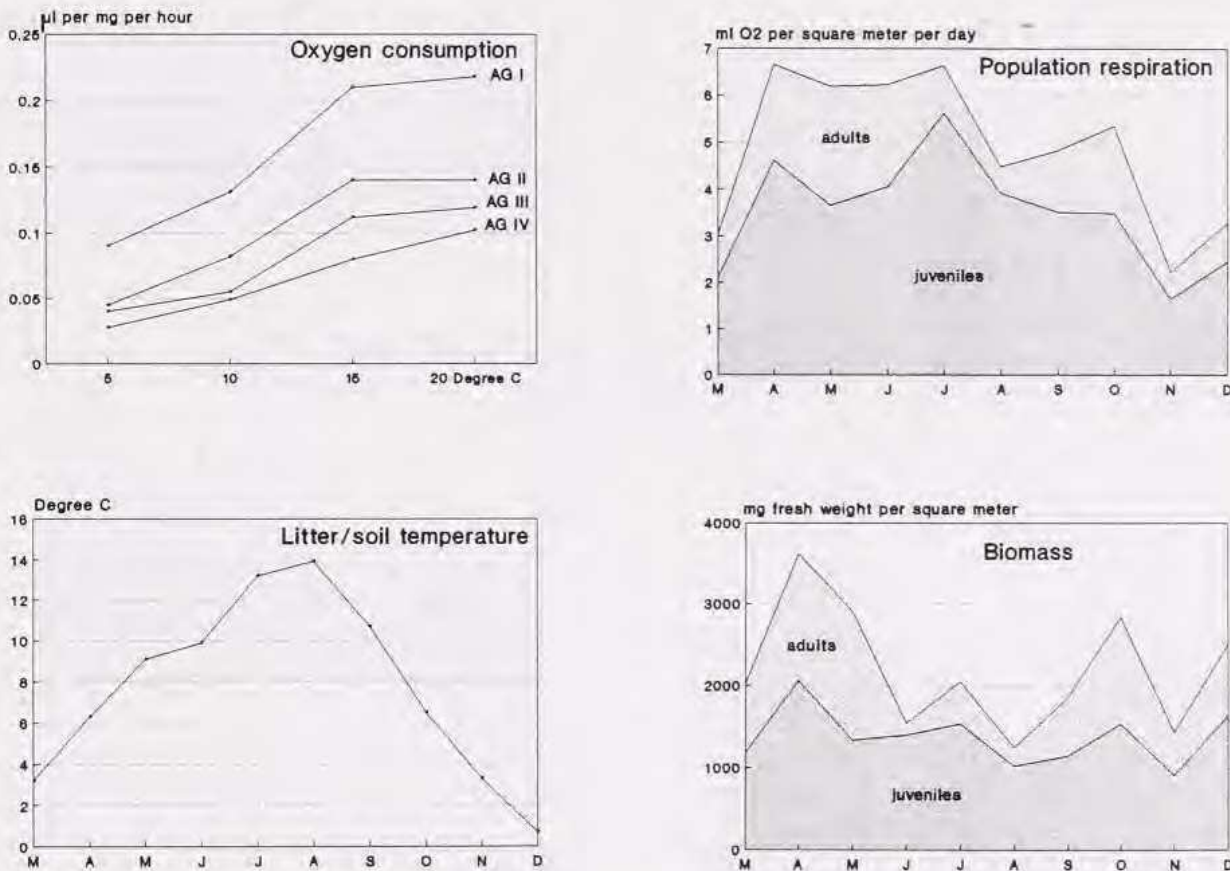


FIG. 2. — Top left: The relationship between oxygen consumption and temperature for the four age groups (AG) of *E. nanus*. The size range of the different groups are given in Table 1. Bottom left: Mean monthly temperature in the litter layer of the oak wood. Bottom right: Mean monthly biomass of juveniles (age group I, stage II-VIII) and adults (age group II - IV, stage IX-XIV) of *E. nanus* in the oak wood (taken from KOFLER & MEYER 1992). Top right: Oxygen consumption by the whole population over the period March-December.

*Enantiulus nanus* (Latzel, 1884) (Fig. 2)

The sum of estimates for each age group gives a total oxygen consumption of 1488 ml O<sub>2</sub> m<sup>-1</sup> year<sup>-1</sup> (= 30 KJ m<sup>-1</sup>) for the population of *E. nanus* in the oak wood. The graphical presentation of the data provides an impression of the relationships between the field temperatures, the dynamics of the biomass and the population metabolism during the vegetation period. Highest total respiration rates are obtained between April and July. In spite of declining biomass due to the disappearance of adults (but favoured by the rising temperature) the population metabolism stays on the same level in the first half of the year. The second biomass peak during October brings the population metabolism again nearly to the same level. The portion attributable to juvenile metabolism is 59-88% in the total population and it is highest in July and August when the new generation is appearing. Adults show their highest respiration rates in May and June during the egg-laying period.

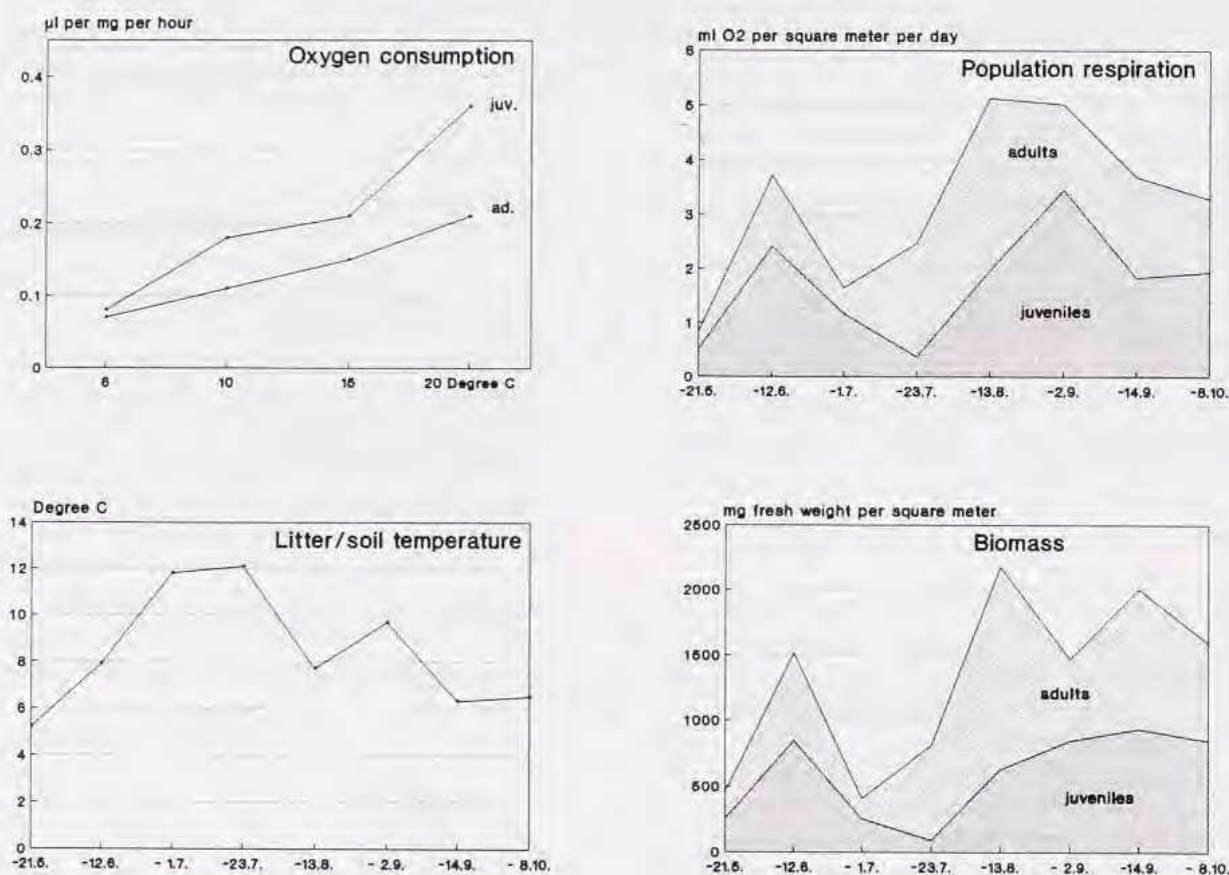


FIG. 3. — Top left: The relationship between oxygen consumption and temperature for juveniles and adults of *L. saltuvagus*. The size range of the two groups are given in Table 2. Bottom left: Mean monthly temperature in the litter layer of the *Alnetum viridis* at 2000 m a.s.l. Bottom right: Mean monthly biomass of juveniles (stage III-VIII) and adults (stage IX-XI) of *L. saltuvagus* in the *Alnetum viridis* (taken from MEYER, 1985). Top right: Oxygen consumption by the whole population over the period May-October.

*Leptoiulus saltuvagus* (Verhoeff, 1898) (Fig. 3)

For the population of *L. saltuvagus* living in alder litter at the timberline, an annual respiratory metabolism of 528 ml O<sub>2</sub> m<sup>-1</sup> (= 10.6 kJ m<sup>-1</sup>) was calculated. According to the fluctuations in biomass, the oxygen consumption is highest in late summer and autumn. The

period with highest litter temperatures (July) does not become apparent in the population metabolism because at that time the population structure undergoes the yearly change. Overwintered adults disappear, overwintered juveniles are probably moulting and the "this-year's" generation has not yet hatched. The portion attributable to juvenile metabolism is 53% in the total population on average with highest values in spring and autumn.

*Ochogona caroli* (Rothenbühler, 1900) and *Haasea fonticolum* (Verhoeff, 1910)  
(Figs 4 and 5)

Total population metabolism of these two Chordeumatida is low. (*O. caroli*: 99 ml O<sub>2</sub> m<sup>-1</sup> year<sup>-1</sup>, (= 1.9 KJ m<sup>-1</sup>); *H. fonticolum*: 105 ml O<sub>2</sub> m<sup>-1</sup> year<sup>-1</sup> (= 2.1 KJ m<sup>-1</sup>). In correspondence with the biomass, highest respiratory rates are obtained in September and October when juveniles and adults occur in large numbers. Adults are short-lived and die in the early spring. 78% (79%) of the total population respiration per year is attributable to the juveniles.

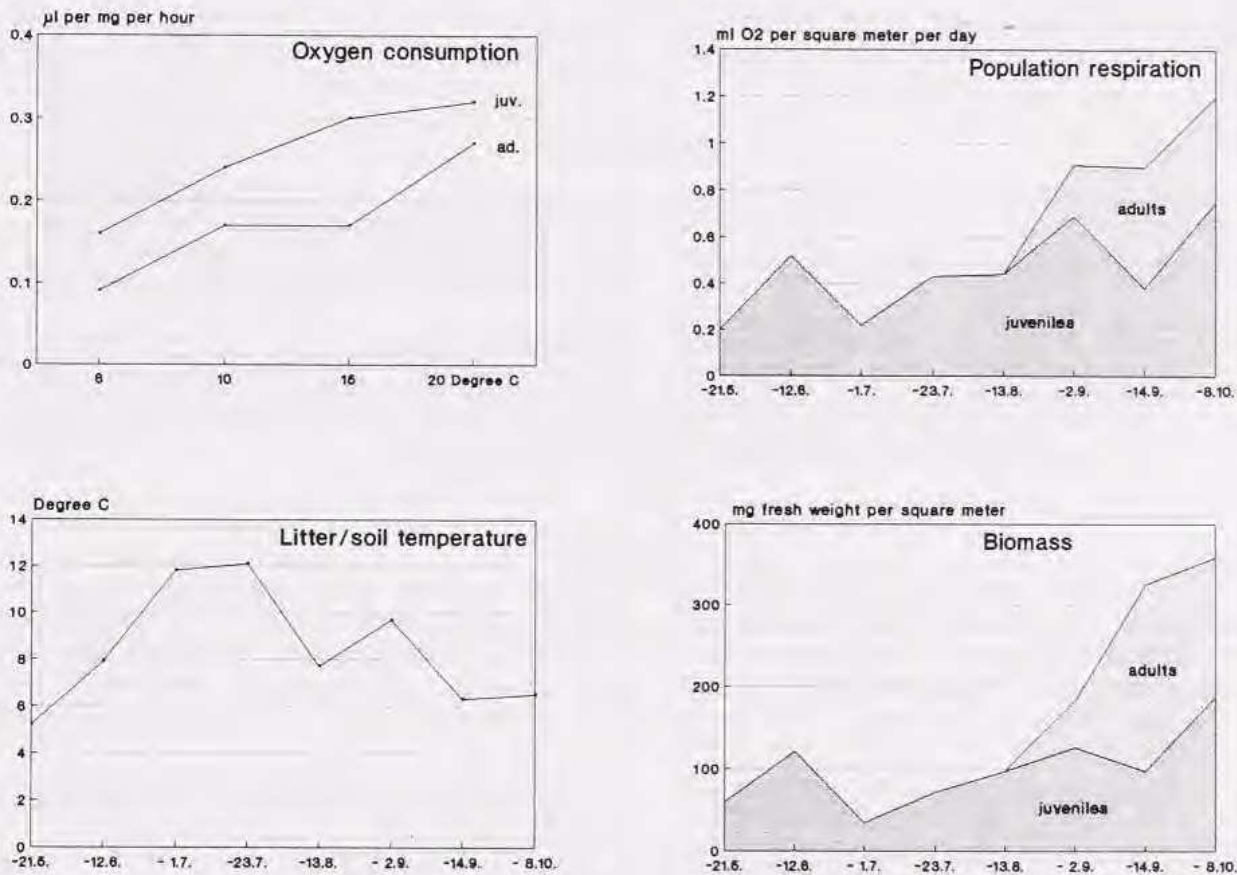


FIG. 4. — Top left: The relationship between oxygen consumption and temperature for juveniles and adults of *O. caroli*. The size range of the two groups are given in Table 3. Bottom left: Mean monthly temperature in the litter layer of the *Alnetum viridis* at 2000 m a.s.l. Bottom right: Mean monthly biomass of juveniles (stage II-VIII) and adults (stage IX) of *O. caroli* in the *Alnetum viridis* (taken from MEYER, 1979). Top right: Oxygen consumption by the whole population over the period May-October.

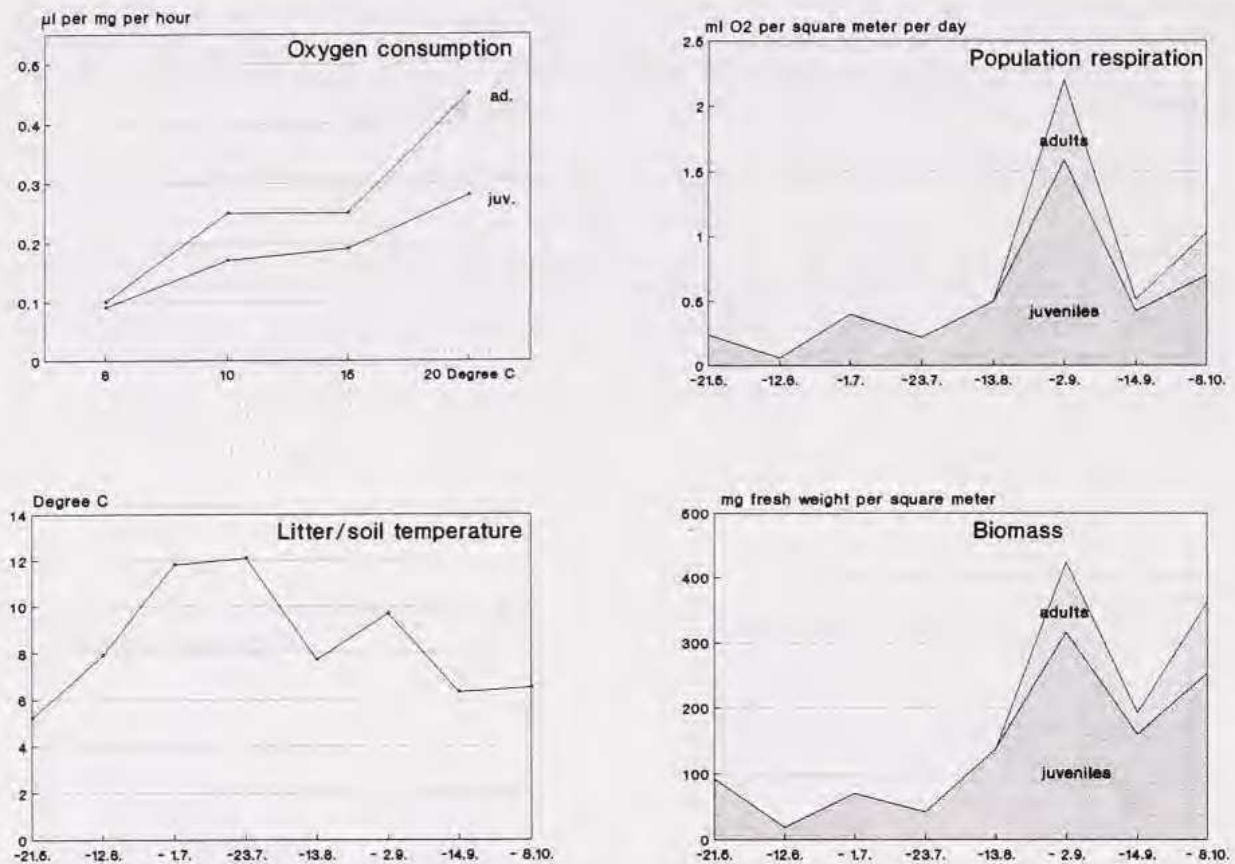


FIG. 5. — Top left: The relationship between oxygen consumption and temperature for juveniles and adults of *H. fonticulatorum*. The size ranges of the two groups are given in Table 4. Bottom left: Mean monthly temperature in the litter layer of the *Alnetum viridis* at 2000 m a.s.l. Bottom right: Mean monthly biomass of juveniles (stage II-VIII) and adults (stage IX) of *H. fonticulatorum* in the *Alnetum viridis* (taken from MEYER 1979). Top right: Oxygen consumption by the whole population over the period May-October.

#### DISCUSSION

The results presented above show that in all species there is a relationship between the respiratory rate and size of individual with b-values ranging from 0.2 to 0.92 depending on species and experimental temperature. Only in *H. fonticulatorum* does the exponent exceed the known range (0.1 - 1.2, as summarised by PENTEADO *et al.*, 1991) reaching values of 1.41-1.67. The measurements coincided with the usual high autumnal activity of this species in its habitat.

The effects of temperature on millipede metabolism have been studied in several species by GROMYSZ-KALKOWSKA & STOJALOWSKA (1966) and GROMYSZ-KALKOWSKA (1970, 1973, 1974). As in many other invertebrates (WIESER, 1973) there is no continuous increase in oxygen consumption with increasing temperature. "Balanced" respiratory metabolism was found within different temperature ranges depending on the species. Such temperature-insensitive phases frequently occur around the mean temperature to be expected in the environment where the species is active. Such a phenomenon could also be demonstrated during the present study. The oak wood species *E. nanus* shows its "temperature-insensitive" phase between 15°C and 20°C with a  $Q_{10}$  of 1.21. This reaction is not fully explained by the temperature conditions in its



habitat, as the daily maxima certainly exceed 15°C for approximately 60 days between June and August, but in no month does the mean temperature reach 15°C (Fig. 3). In the lower temperature range between 10°C and 15°C the  $Q_{10}$  is 3.08. This great sensitivity to temperature changes allows the animal to speed up its metabolism as much as possible following hibernation or coldness. Consistently the three subalpine species (*L. saltuvagus*, *O. caroli* and *H. fonticularum*) have their greatest sensitivity to temperature changes between 6°C and 10°C with  $Q_{10}$  values of 7.9, 3.2 and 7.2. In their habitat at the timberline wet weather is often accompanied by coldness and snowfall even in the summer. Large and rapid temperature changes often occur during the vegetation period. Between June and September the oscillations of the daily mean temperatures in the litter layer of *Alnus viridis* are mostly between 5°C and 10°C (MEYER, 1990). A high sensitivity in this temperature range must be ecologically significant and allows the millipedes to exploit warmer periods efficiently in the overall short growth period. The temperature-insensitive phase of these species occurs between 10°C and 15°C with  $Q_{10}$  values of 1.1, 1.5 and 1.2.

Figures 2-5 allow the comparison of the relative influences of the factors temperature, age structure and biomass affecting the final estimates of the population metabolism. In all species the seasonal changes in oxygen consumption of the population reflects changes in population structure and biomass much more than changes in temperature. Similar observations by HASSALL (1983) during investigations into the population metabolism of the isopod *Philoscia muscorum* led to the suggestion that the accuracy with which the population structure and biomass can be assessed is likely to be the most important single factor in determining the metabolism for field populations.

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